INVASION OF *PINUS CONTORTA* VAR. *MURRAYANA* (PINACEAE) INTO MOUNTAIN MEADOWS AT YOSEMITE NATIONAL PARK, CALIFORNIA

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ABSTRACT

Stands of *Pinus contorta* var. *murrayana* (lodgepole pine) at the edge of many meadows have a tiered appearance due to bands of trees of increasing size class. Factors that might contribute to these waves of encroachment are seed availability and seedling establishment. Seed fall and distribution were monitored on two meadows in Yosemite National Park, California. Approximately 10,000–135,000 seeds/ha were distributed annually across the meadows. This probably represents 2–13% of seeds that fall commonly within lodgepole pine stands. First-year seedlings were estimated to be 550–10,000/ha annually. None of the naturally-established seedlings in the sample plots survived through the third growing season. Thus, waves of encroachment are more likely the result of success in establishment than of inadequate numbers of seeds or short dispersal distance. Nine 26–40 m transects from the meadow edge into the adjacent forest showed distinct periods of encroachment. On the wetter meadow these were 1950–1962 and 1918–1936. A comparison with records of precipitation available since 1907 shows that the two most recent periods of encroachment are associated broadly with periods of lesser precipitation. On the drier meadow, periods of encroachment were less distinct, but occurred during 1948–1973 and 1905–1931. Drier meadows are more conducive to pine establishment and encroachment is influenced less by patterns of precipitation.

Many mountain meadows in the Sierra Nevada, particularly the smaller, drier ones, are being invaded gradually by *Pinus contorta* var. *murrayana* (Grev. & Balf.) Engelm. (lodgepole pine) (DeBenedetti and Parsons 1979a). Invasion of meadows is a natural, dynamic process, but the factors that influence the rate of meadow invasion are not well understood. The phenomenon is of managerial and ecological interest. Conversion of meadows to stands of lodgepole pine reduces ecological diversity with adverse impacts on scenic, recreational, habitat, and grazing values.

Lodgepole pine in the Sierra Nevada is a prolific seed producer with crops of non-serotinous cones produced annually (Critchfield 1980). Seed fall in south-central Oregon has varied from 12,000 to over 2 million seeds/ha (Dahms and Barrett 1975). Although lodgepole pine has small seeds that are among the most dispersible of any North American conifers (Critchfield 1980), density of seedfall at a distance of 20 m from the timber edge may be only 10–30% of that within the stand, and most seeds fall to the ground within a distance of about 60 m (Lotan 1975, Lotan and Critchfield in press).

MADROÑO, Vol. 34, No. 2, pp. 91–97, 1987

Invasion of lodgepole pine into meadows appears to be associated with warm-dry weather, grazing, and fire. The relative dryness of meadow soils is associated with the amount of snow and timing of snowmelt, which in turn are affected by the size and orientation of meadows (Anderson 1967). Similarly, Wood (1975) suggests that lodgepole pine seedlings tend to become established in years of low snowpack and that invasion patterns are affected by water table fluctuations. In the southern Sierran region, for example, changes in meadow vegetation are commonly associated with geological instability that in turn causes changes in water status (Benedict 1982). Vale (1981) concluded that although warm-dry weather is cited often as a major factor influencing lodgepole pine invasion into meadows, climatic fluctuations are typically less important than grazing or fire. Meadow disturbances from livestock grazing and trampling favors the establishment of pine seedlings, but also retards their development. Pines rapidly encroached into meadows when intensive sheep grazing ceased in 1900. Similarly, pine invasion into meadows of Kings Canyon National Park followed after the expiration of cattle grazing permits in the mid-1950's (Sharsmith 1959). Fire due to lightning strikes in grazed areas or due to the activities of Indians also influenced pine regeneration in meadows (DeBenedetti and Parsons 1979b).

I conducted this study to better understand the factors that influence the rate and timing of lodgepole pine invasion into meadows. My objectives were to determine 1) the dispersion of lodgepole pine seed into meadows from neighboring stands, 2) the extent of seed germination and establishment, and 3) the patterns of rate and timing of past lodgepole pine invasion into meadows.

Methods

The large and small meadows selected for this study are located at 2100 m in Yosemite National Park, California, near Glacier Point Road on the trail to Lost Bear Meadow. They are the same meadows used for a concurrent study of lodgepole pine germination and establishment (Helms and Ratliff 1987). Detailed description of meadow physiography, soils, and vegetation are presented in that paper.

Natural seed dispersal. A sampling system of 195 and 95 seed traps was installed in the large and small meadows, respectively, in the fall of 1981, 1982, 1983, and 1984. They were in position from mid-August until snowfall was imminent in October. Traps were 0.1 m^2 in size, made of 2.5-mm-mesh wire screen, and positioned 1 m above the ground on a 10 × 10 m grid. The grids extended from the southern to the northern edge, and were located in the eastern half of each meadow.

TABLE 1. NUMBERS OF SEEDS/HA (± s.e.) DISTRIBUTED IN EACH MEADOW IN FOUR SUCCESSIVE YEARS.

Year	Large meadow	Small meadow
1981	28,830 ± 6080	134,560 ± 14,940
1982	23,240 ± 4090	125,945 ± 14,830
1983	9620 ± 2850	24,760 ± 6060
1984	20,861 ± 8800	26,911 ± 9300

Natural seedling establishment. A 0.1 m^2 plot was established 1 m north of each seed trap location. This provided a sample of 195 plots on the large meadow and 95 plots on the small meadow. Each fall, from 1982 through 1984, plots were examined for the presence of lodgepole pine seedlings.

Encroachment of lodgepole pine into meadows. Five transects were established in the large meadow and four in the small meadow. Each transect was 26–40 m long and extended from the meadow edge into the adjacent forest. Along each transect, 15–20 trees were measured in terms of height and distance from meadow edge. The age of each tree was determined by extracting a core from the stem at ground level and counting annual rings. Approximately 20 representative outlier trees within each meadow also were measured.

RESULTS

Natural seed dispersal. In each study year, a substantial cone crop was observed on the dominant trees with exposed crowns. Cone opening occurred on warm fall days. In the large meadow, the proportions of seed traps containing seeds in 1981, 1982, 1983, and 1984, were 17, 16, 6, and 23%, respectively. In the small meadow, the corresponding proportions in each year were 65, 88, 18, and 12%, respectively. The average annual seed fall on the large and small meadow over the four year period was 10,000–29,000 and 25,000–135,000 seeds/ha, respectively (Table 1). In the 80-m-wide small meadow, substantially more seeds were distributed within 30 m of the meadow edges than in the center of the meadow. This trend was not found in the large 220-m-wide meadow where the seeds were distributed more evenly.

Natural seedling establishment. In the large meadow, the total numbers of seedlings found in the 195 plots in 1982, 1983, and 1984 represent 550, zero, and 2200/ha, respectively. This is equivalent to two, zero, and 22% of seeds dispersed in the previous year (Table 1). On the small meadow, the total numbers of seedlings found in the 95 plots in the same years represent 4500, 4500, and 10,200/

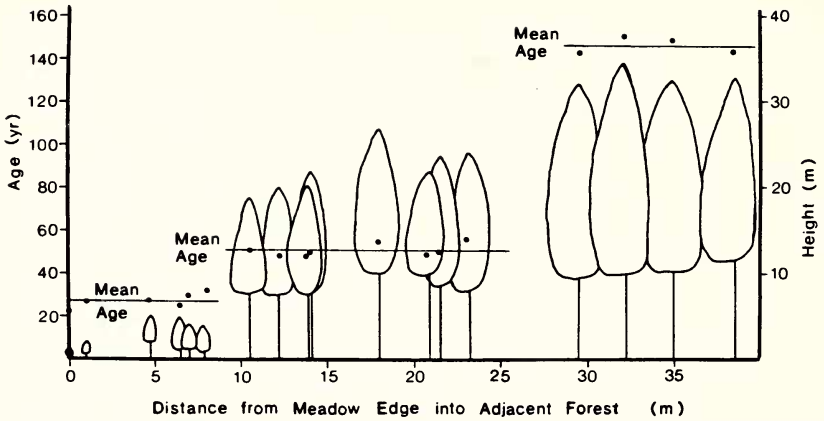

FIG. 1. Typical distribution of height- and age-classes in meadow-edge lodgepole pine of the large meadow.

ha, respectively, or 3%, 3%, and 41% of seeds dispersed in the previous year (Table 1).

In both meadows, the highest first-year survival occurred in 1984, which followed the smallest seed crop measured during the 4 yr study. All seedlings observed over the 3 yr of the study were ephem-

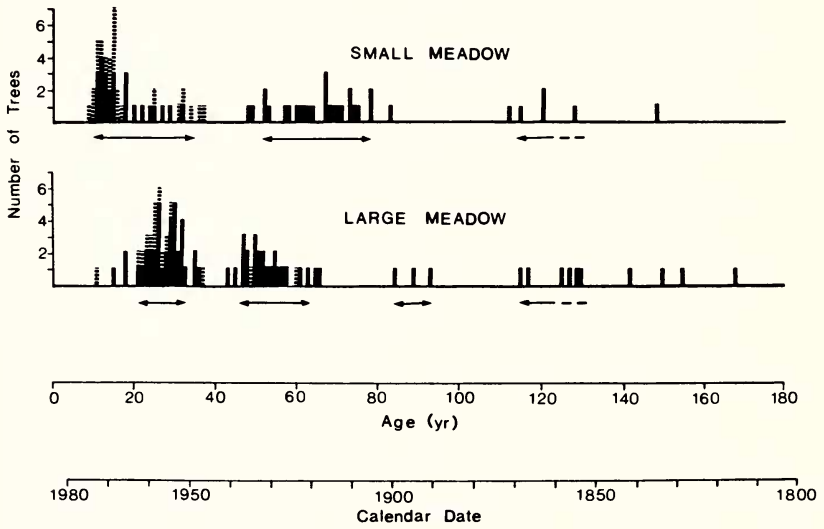

FIG. 2. Frequency distribution of age classes of meadow-edge trees (solid bars) from a total of nine 26–32 m transects, and all outlier lodgepole pine trees (hatched bars) in both the large and small meadows. Arrows indicate periods during which most encroachment of meadows occurred.

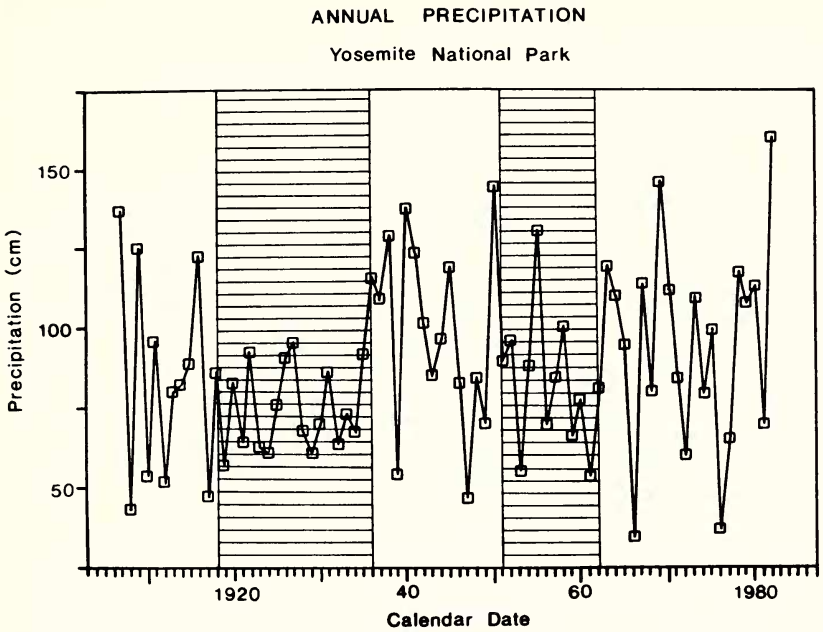

FIG. 3. Complete record of annual precipitation at the valley floor, Yosemite National Park, California. Hatched areas show periods during which most lodgepole pine encroached on the larger, wetter meadow.

eral. In only one case did a seedling survive into year two, but it did not survive through the third season.

Encroachment of lodgepole pine into meadows. The typical pattern of meadow-edge trees contained distinctly different age and height classes (Fig. 1). The large meadow was bordered by trees of two age classes: 21–33 and 47–65 yr and some older individuals that ranged from 80–170 yr (Fig. 2). These waves of encroachment occurred in the periods: 1950–1962 and 1918–1936, with older trees having become established prior to 1900. The small meadow was bordered by two, less distinct age classes: 10–35 and 50–80 yr and some older individuals that ranged from 115–150 yr. These age classes represent waves of encroachment occurring in 1948–1973 and 1905–1931, and some older trees established prior to 1860.

In the large meadow, two classes of outlier trees were identified: 1) 23.8 ± 1.3 yr and 6.02 ± 0.53 m in height, and 2) 49.0 ± 4.1 yr and 11.97 ± 0.79 m in height. These two classes correspond to the two youngest age classes of meadow-edge trees (Figs. 1 and 2). In the small meadow, the corresponding two classes were: 1) 13.6 ± 0.5 yr and 1.5 ± 0.13 m in height, and 2) 34.5 ± 1.1 yr and 12.68 ±

0.46 m in height. These two classes occur within the youngest age class of meadow-edge trees (Fig. 2).

No relationship was found between age of outlier tree and distance from the meadow edge. Outliers were located on slightly higher, drier locations within the meadows.

Correlation between encroachment and precipitation patterns. The periods during which most encroachment occurred on the larger, wetter meadow (Fig. 2) were superimposed on a complete record of annual precipitation (1907–1984) in Yosemite Valley (Fig. 3). Average precipitation during periods of no encroachment was 97.1 ± 5.4 cm. In comparison, average precipitation during periods of successful regeneration, was 80.5 ± 3.2 cm. The difference between these means was significant ($p \leq 0.02$). The smaller, drier meadow, in which channel erosion had lowered the water table, showed no apparent correlation between encroachment and precipitation.

Discussion

Encroachment of pine seedlings into meadows was limited by lack of seedling survival rather than by inadequate seed supply or insufficient numbers of seedlings. In the large meadow, seeds distributed in the fall that escape predation may be washed away by free-flowing water that generally covers parts of the meadow until mid-summer. Invasion of lodgepole pine into meadows, therefore, is more likely at the meadow edge where there is higher seed fall and less flooding. The similar ages of both edge trees and outlier trees within the meadows suggests that conditions favorable for pine establishment in both locations occur concurrently.

The association between periods of most encroachment of lodgepole pine and periods of less precipitation (Fig. 3) is not strong, but provides support for the concept that invasion occurs under drier conditions.

In a study of lodgepole pine invasion near the Tioga Pass entrance to the park, the oldest tree found was established in 1866 (Vale 1981). Most trees were established from 1910–1975. No distinct pattern of invasion was found; however, most trees were established in 1925. Other periods reported to be associated with invasion are 1853–1875 and 1898–1909 (Boche 1974), 1910 (Vankat and Major 1978), and 1903, 1906, and 1924 (Wood 1975). Results of the present study suggest that variability in reported periods during which invasion occurred may be associated with wetness and size of meadow.

Rates of encroachment from 1868–present, determined by the relationship between age of trees and distance from the meadow edge, were 0.19 and 0.22 m yr^{-1} for the large and small meadow,

respectively. At a similar rate of encroachment and with current meadow conditions the larger and smaller meadows will be invaded completely within ca. 580 and 180 yr, respectively.

Acknowledgments

This study was supported by the USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, Project Number PSW-80-0022. It also was part of the University of California's Agricultural Experiment Station Project 2942-MS. I thank Drs. W. Critchfield and F. Vasek for their helpful suggestions to improve the manuscript.

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(Received 6 Sep 1985; revision accepted 15 Dec 1986.)